A new basal snake from the mid-Cretaceous of Morocco

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Abstract

Fossil snakes are relatively well represented in the Upper Cretaceous of northern Africa, with material known from Morocco, Sudan, Egypt, Libya, Algeria, and Niger. The Moroccan Kem Kem beds yield a particularly diverse snake assemblage, with Simoliophiidae, Madtsoiidae, ?Nigerophiidae and several unnamed taxa co-occurring. These fossils are important for our understanding of the early evolutionary history of snakes, and may shed light on the ecology and initial diversification of basal snakes. We describe a new taxon, *Norisophis begaa* gen. et sp. nov., from the Kem Kem beds of Begaa, in southeast Morocco. It is characterised by a marked interzygapophyseal constriction, parazygantral foramina, an incipient prezygapophyseal process, and an anterio-posteriorly short centrum. Several characteristics shared with *Najash, Seismophis,* Madtsoiidae*,* and *Coniophis* suggest that *Norisophis* is a stem ophidian. *N. begaa* further increases the diversity and disparity of snakes within the Kem Kem beds, supporting the hypothesis that Africa was a mid-Cretaceous hotspot for snakes.

Keywords: Cretaceous, Ophidia, Serpentes, Kem Kem, Morocco

1. Introduction

Snakes are a highly successful clade of reptiles, occupying all continents except Antarctica and represented today by approximately 3,400 species (Hsiang et al. 2015; Greene 1997). The origin and early evolutionary history of snakes, however, remains poorly understood. In contrast to their extant diversity, there is a dearth of fossil data for the Serpentes stem and at the base of the crown group, hindering attempts to reconstruct phylogenetic relationships, the timing of divergence events, and the ecology of early snakes (Hsiang et al. 2015). Considerable debate has stemmed from this, most notably about whether snakes originated in Laurasia or Gondwana, and whether the snake body plan originated in a terrestrial or marine context (Hsiang et al. 2015; Martill et al. 2015; Lee et al. 2016; Longrich et al. 2012a; Rieppel et al. 2003).

The geographical origin of snakes continues to be a subject of discussion. Iguania and Anguimorpha, recovered as closest relatives to Serpentes by phylogenetic analyses using molecular or combined molecular and morphological data (Pyron et al. 2013; Vidal & Hedges 2009; Zheng & Wiens 2016; Wiens et al. 2012; Reeder et al. 2015; Mulcahy et al. 2012), appear to originate in Laurasia (Benson et al. 2013; Vidal & Hedges 2005). Furthermore, the putative early snakes *Parviraptor, Diablophis, Eophis* and *Portugalophis*, dating from ~ 167 – 155 Ma, are from Laurasia (Caldwell et al. 2015), as is the definitive stem snake *Coniophis precedens* (Marsh 1892). However, many of the earliest definitive ophidians, including the Nigerophiidae, Lapparentophiidae, *Seismophis, Lunaophis, Dinilysia,* and *Najash* are Gondwanan (de Broin et al. 1974; Woodward 1901; Rage & Albino 1989; Zaher et al. 2009; Apesteguía & Zaher 2006; Rage & Escuillié 2003; Albino et al. 2016), whilst the Madtsoiidae and Simoliophiidae are present on both supercontinents (Vasile et al. 2013; Rage 1996;

Mohabey et al. 2011; Rage & Dutheil 2008; Rage et al. 2016; Nessov et al. 1998; Rieppel et al. 2003; Rage & Escuillié 2003). A recent biogeographical analysis using ancestral state reconstruction suggests that the situation is complicated, with the snake total group probably having originated in Laurasia, but the crown group originating in Gondwana (Hsiang et al. 2015).

Another focus of debate is whether snakes evolved on land, or in the oceans. Some evidence points towards an aquatic origin, such as a potentially close relationship between snakes and mosasaurs (Martill et al. 2015; Reeder et al. 2015; Lee 1997; Lee 1998), and the existence of aquatic taxa such as the Simoliophiidae (Rage & Escuillié 2003; Lee et al. 1999; Caldwell & Lee 1997; Rage & Escuillié 2000; Tchernov et al. 2000), Nigerophiidae (Rage 1975), and *Lunaophis* (Albino et al. 2016). However, evidence increasingly points towards a terrestrial origin, an hypothesis that is supported by ancestral state reconstruction (Hsiang et al. 2015), the resemblance of the inner ear of *Dinilysia* to that of burrowing squamates (Yi & Norell 2015), and new fossils such as *Tetrapodophis amplectus*, a four-limbed snake that shows adaptations for burrowing (Martill et al. 2015; Lee et al. 2016).

The mid-Cretaceous of North Africa provides a window into snake evolution around crown Serpentes, and can potentially help answer some of these questions. Multiple localities in North Africa produce mid-Cretaceous fossil snakes, including the Moroccan Kem Kem beds (Rage & Dutheil 2008), the Wadi Milk Formation of Sudan (Rage and Werner, 1999; although some recent evidence suggests that this fauna could be Maastrichtian or Campanian-Maastrichtian in age; Eisawi et al., 2012; Eisawi, 2015; Klein et al., 2016), the Bahariya Formation in Egypt (Nopcsa 1925), the Mizdah Formation in Libya (originally assigned to the Maastrichtian by Nessov et al., 1998, but then referred to the Cenomanian by Rage and Cappetta, 2002), and the “série d’In Akhamil” of Algeria (Cuny et al. 1990). Simoliophiidae,

Madtsoiidae, and Nigerophiidae are present in these localities, as well as several ophidian taxa of uncertain affiliation.

Among the most productive of these localities are the Kem Kem beds of southeastern Morocco. Vertebrate fossils in the Kem Kem beds are typically preserved as isolated elements, associated skeletons being very uncommon (Ibrahim, Sereno, et al. 2014). The beds are particularly well known for the abundance and diversity of their large vertebrate assemblage, which includes crocodylomorphs (Sereno & Larsson 2009), theropod and sauropod dinosaurs (Mannion & Barrett 2013; Ibrahim, Sereno, et al. 2014; Sereno et al. 1996; Russell 1996), and large pterosaurs (Ibrahim et al. 2010). Giant predatory dinosaurs (e.g. *Spinosaurus*, *Carcharodontosaurus*) are unusually abundant (Ibrahim et al. 2016), but no ornithischian dinosaur postcranial elements or teeth have been recorded (see Ibrahim et al., 2014b for possible ichnological evidence). The fauna is also rich in fishes and non-archosaurian reptiles and amphibians, with elasmobranchs, actinopterygians, at least one species of salamander, several species of frogs and turtles, an iguanian and an undetermined lizard, and snakes reported (Cavin et al. 2010; Rage & Dutheil 2008; Apesteguía et al. 2016).

At least four snake clades occur in the Kem Kem beds: Simoliophiidae, Madtsoiidae, ?Nigerophiidae, and an undetermined snake (Rage & Dutheil 2008). Remains are locally abundant, with dozens of simoliophiid specimens reported by Rage and Dutheil (2008). Here, we describe a further snake genus, distinct from those previously reported by Rage and Dutheil (2008), further increasing the diversity of the Kem Kem snake fauna.

2. Geological Setting

The Kem Kem beds represent a continental deposit (Dutheil 1999) unconformably overlying Palaeozoic basement units. The sequence exceeds 200 m in thickness in some localities. It is dominated by arenaceous fluvial deposits for approximately two-thirds of the sequence, with the upper part being overbank muds and silty channel deposits, probably accumulating in a muddy estuary or embayment. Vertebrate fossils primarily occur in the sandy beds. The Kem Kem beds are overlain by carbonates of the Akrabou Formation, which is of late Cenomanian/Turonian age. The age of the Kem Kem beds is imprecisely known: over the last few decades, the age of the Kem Kem sequence has been regarded variously as Albian, Albo-Cenomanian or Cenomanian (Riff et al. 2002; Dutheil 1999; Russell 1996). Some workers currently consider the beds to be Cenomanian in age (Rage & Dutheil 2008; Ibrahim et al. 2010), although its lower portion may lie within the Albian (Taquet 1980; Forey & Grande 1998).

3. Materials and methods

The specimens described here come from the Kem Kem sequence of southeastern Morocco, in Begaa and Aoufous, in the Province d'Errachidia (Fig. 1.). All material is housed at the Faculté des Sciences Aïn Chock (FSAC), Université Hassan II, Casablanca, Morocco. Vertebrae were prepared using mounted needles, and photographed with a digital camera (Cannon EOS 5D fitted with an MP-E 65 mm macro lens). Macro focusing rails were used to photograph smaller vertebrae at different heights, and resultant images were stacked using the free software Inkscape v.0.91 (www.inkscape.org).

4. Results

4.1 Systematic palaeontology

Order: Squamata Oppel, 1811

Suborder: Ophidia Brogniart, 1800

Genus: *Norisophis* gen. nov.

Type species: *Norisophis begaa* sp. nov.

Etymology. From Greek, *norís*, meaning early, and *ophis*, snake

Diagnosis. Differs from other Cretaceous snake species by exhibiting the following combination of characters: faint or absent interzygapophyseal ridges; marked interzygapophyseal constriction; presence of parazygantral foramina; mid-trunk vertebrae short; neural spine rudimentary; large paradiapophyses which extend dorsally almost to the incipient prezygapophyseal ridge.

Norisophis begaa gen. et sp. nov.

Etymology. "begaa", meaning from the desert oasis of Begaa.

Type material. Holotype: FSAC-KK 7001, a posterior trunk vertebra with all zygapophyses preserved, but some erosion of the paradiapophyses (see Fig. 2.). Paratypes: FSAC-KK 7004, FSAC-KK 7005 two mid-trunk vertebrae (see Fig. 3.).

Locality and horizon. Kem Kem beds of Begaa, east of Taouz, southeastern Morocco (see Fig. 1.), ?Cenomanian. Locality Aferdou N'Chaft (30°53'57" N, 3°50'46 W), or Aferdou n'Bou Tarif (30°53'12" W, 3°52'29" W), in the Ifezouane Formation.

Diagnosis. As for the genus, by monotypy.

Description. The vertebrae originate from a moderately sized snake. In the posterior trunk region, the holotype vertebra is wider (7.46 mm) than long (7.02 mm), unlike *Coniophis* (Marsh 1892; Longrich et al. 2012a) and Russellophiidae (Rage & Werner 1999; Rage et al. 2008). This is even more pronounced in mid-trunk vertebrae (see Fig 3). In anterior view, the

holotype vertebra appears laterally expanded. Overall, the vertebrae are relatively robust, with very strong interzygapophyseal constriction. The holotype is a posterior trunk vertebra. There is little variation between the holotype and the referred material, although very slight differences in the angling of the zygapophyses and zygosphene can be seen between FSAC-KK 7001, and FSAC-KK 7004 and FSAC-KK 7005.

Despite the underdeveloped neural spine, the vertebrae still increase in height posteriorly, unlike in *Seismophis septentrionalis* (Hsiou et al. 2014). A poorly defined neural ridge extends anteriorly to the posterior border of the zygosphene, visible especially in the referred vertebra FSAC-KK 7004. The neural arch is low as in *Nidophis*, a madtsoiid (Vasile et al. 2013), with the neural spine occupying only the posteriormost quarter, making it much less developed than that in all Madtsoiidae except *Herensugea caristiorum* (LaDuke et al. 2010; Rage 1996; Wilson et al. 2010). Faint laminar crests extend to the posterior border of the vertebrae. These neural arch laminae barely protrude above the dorsal aspect of the postzygapophyses in posterior view, making them much less developed than in posterior trunk vertebrae in *Dinilysia* (Rage & Albino 1989).

Dorsally, the zygosphene in *N. begaa* has a rectilinear roof. It is less well developed than that of *Coniophis*, and narrows more ventrally (Hecht 1959; Armstrong-Ziegler 1978; Longrich et al. 2012a). The zygantrum is prominent, with the depressions being almost triangular in the holotype. On either side there are small parazygantral foramina, as in the madtsoiids *Sanajeh indicus* (Wilson et al. 2010) and *Nidophis insularis* (Vasile et al. 2013), as well as *Najash rionegrina* (Apesteguía & Zaher 2006; Zaher et al. 2009). The foramina are situated ventrally from a notch projecting laterally from the dorsal limit of the articular surfaces of the zygantrum.

182 The prezygapophyses are laterally angled dorsally and reach the upper half of the coronal
183 plane of the zygosphene, thus reaching higher than in *Dinilysia* (Scanferla & Canale 2007). The
184 prezygapophyseal processes are incipient, differentiating *Norisophis* from *Najash* and the
185 Madtsoiidae (Rage 1996; Vasile et al. 2013; LaDuke et al. 2010; Zaher et al. 2009; Apesteguía
186 & Zaher 2006). In dorsal view, the prezygapophyses extend wider laterally than the
187 postzygapophyses. The latter have small protuberances on the posterior margin of the neural
188 arch, between the neural spine and postzygapophyses. When viewed laterally, the articular
189 surfaces of the zygapophyses are at the same height. The interzygapophyseal constriction is
190 marked, although the holotype remains wider at the interzygapophyseal constriction than it is
191 long. There is no interzygapophyseal ridge.
192
193 The parapophyses and diapophyses are undivided, dorsally reaching above the cotylar rim,
194 starting just 1-2 mm below the prezygapophyses. Compared to other taxa such as *Coniophis,*
195 *Najash, Madtsoia, Nidophis* and *Herensugea*, the paradiapophyses occupy a larger relative area
196 on the centrum (Longrich et al. 2012a; Marsh 1892; Zaher et al. 2009; Apesteguía & Zaher
197 2006; Vasile et al. 2013; Rage 1996). They project more laterally than in *Najash rionegrina*
198 (Zaher et al. 2009), and almost reach the prezygapophyseal tip. Ventrally, one of the
199 parapophyses reaches the cotylar rim. Although eroded, the paradiapophyses appear mostly
200 oriented laterally. The paradiapophyses are generally rectangular, taller than wide, with a
201 slight distinction between the diapophysis and parapophysis visible.
202
203 The cotyle is dorso-ventrally flattened, the widest point being below the midline, and is
204 angled dorsally. Shallow paracotylar depressions are present in all vertebrae, but paracotylar
205 foramina are only present in FSAC-KK 7005. Unlike Simoliophiidae (Rage & Dutheil 2008;
206 Rage et al. 2016), Madtsoiidae (Mohabey et al. 2011; Rage 1996; Vasile et al. 2013), and crown
207 Alethinopidia, there is no channel between the ventral border of the condyle and the ventral

aspect of the centrum. Instead the condyle and the centrum are confluent, a feature shared with *Coniophis precedens* (Marsh 1892; Longrich et al. 2012a) and *Tetrapodophis amplectus* (Martill et al. 2015).

Posteriorly, the vertebra is still very much dorso-ventrally flattened. The ventral aspect of the vertebra shows a marked gradual constriction of the centrum starting directly behind the paradiapophyses. Lateral foramina are present on the centrum. The haemal keel is broad, with anteriorly-diverging subcentral ridges on either side.

***Norisophis* sp.**

Locality and horizon. From the Kem Kem beds (Aoufous Formation?) just south of Aoufous (31°41'17" N, 4°10'44" W), near Erfoud, Morocco (see Fig. 1.). Although it is not precisely known which bed yielded the fossil, only the Aoufous Formation appears to be collected from at the nearby Douira locality (Cavin et al. 2010).

Description. FSAC-KK 7002 (Fig. 4.) shares the diagnostic features of *Norisophis begaa*. The neural arch is vaulted. The neural spine extends posteriorly from the posterior border of the zygosphene as a shallow ridge, unlike neural spines seen in Madtsoiidae, Simoliophiidae, *Najash,* and *Coniophis* (Vasile et al. 2013; Mohabey et al. 2011; Rage et al. 2016; Rage & Escuillié 2003; Zaher et al. 2009; Apesteguía & Zaher 2006; Longrich et al. 2012a). The small protruberances on the posterior edge of the neural arch are also more pronounced than in the holotype FSAC-KK 7001, seeming to extend to the middle of the vertebra on the right side of FSAC-KK 7002 (see Fig. 4D).

As in *N. begaa,* dorsally the zygosphene has a rectilinear roof. Ventrally, the zygosphene narrows more than *Coniophis* (Longrich et al. 2012a; Marsh 1892), but less so than *Kelsyophis*,

a madtsoiid (LaDuke et al. 2010). The zygantrum is well-formed, with parazygantral foramina. The visible foramen sits higher dorsally than in Madtsoidae (LaDuke et al. 2010).

The zygapophyses are angled as in *N. begaa*, despite being from a more anterior position on the trunk. The prezygapophyseal processes are incipient. The prezygapophyses extend further laterally than the postzygapophyses. The interzygapophyseal constriction is marked, but the vertebra remains wider than it is long. The lateral expansion of the pre- and postzygapophyses start from the same point, with no interzygapophyseal ridge.

The paradiapophyses cover a relatively large area, and dorsally approach the incipient prezygapophyseal ridge. They do not approach the cotylar rim as in *Norisophis begaa*, but do project laterally. Below the prezygapophyses, they project anteriorly further than the cotylar rim. The cotyle is dorso-ventrally flattened and slightly triangular in shape. Paracotylar foramina are absent, unlike *Simoliophis rochebrunei* and *Lapparentophis defrennei* (Rage et al. 2016; Hoffstetter 1959).

The vertebra becomes less dorso-ventrally flattened posteriorly. It displays abnormal bone growth on its ventral side, extending postero-laterally to nearly the dorsal edge of the paradiapophyses, thus obscuring the subcentral ridges and haemal keel. This could be the result of an injury, potentially a fracture of the back.

5. Discussion and conclusions

5.1 Relationships of *Norisophis*.

In *Norisophis begaa,* the anterior margin of the zygosphenal tectum is slightly concave but not notched, and the paradiapophyses appear to be divided into diapophyses and parapophyses. These characters confirm that it is an ophidian (Apesteguía & Zaher 2006). Within snakes, *Norisophis* appears to be a basal member, most likely a stem ophidian.

An unnamed madtsoiid has been described from the Kem Kem beds (Rage & Dutheil 2008). It differs from *Norisophis* in the absence of prezygapophyseal processes, and is described as resembling *Herensugea caristiorum*. *Herensugea* vertebrae are wide and depressed, with a wide and thin zygosphene whose articular facets are relatively horizontally oriented, oval prezygapophyseal facets, a neural spine composed of a posterior tubercle and an anterior keel, very distinct subcentral borders and a wide haemal keel, and very obtuse angling of the posterior border of the neural arch (Rage 1996). It shares with *Norisophis* the overall shape of the vertebrae, the shallow angle of the posterior border of the neural arch, the limited development of the neural arch, and the relative width of the zygosphene and haemal keel. However, *Norisophis* differs from *Herensugea* by having a robust zygosphene with more laterally projecting articular surfaces, prezygapophyseal surfaces which come to a point antero-laterally, the presence of incipient prezygapophyseal processes, and absence of a limited keel on either side of the neural spine. As a result, it seem unlikely that *Norisophis* is the unnamed madtsoiid mentioned by Rage and Dutheil (2008).

N. begaa shares many characteristics with *Coniophis, Najash* and *Dinilysia*, including the very low neural spine, the limited development of the haemal keel, and the lack of a groove separating the ventral aspect of the condyle from the centrum. In contrast to *Coniophis*, *N. begaa* has a slight indentation of the posterior border of the neural arch, and no clearly identifiable haemal carina. It is similar to *Najash* in the presence of parazygantral foramina, but differs in that is has more laterally projecting paradiapophyses, and more pronounced

285 interzygapophyseal constriction (Zaher et al. 2009). Compared to *Dinilysia,* the
286 paradiapophyses extend dorsally much further, the prezygapophyses also extend higher
287 dorsally and almost reach the roof of the zygosphene, and the interzygapophyseal constriction
288 is again more marked in *N. begaa* (Scanferla & Canale 2007).
289
290 Despite the differences present, the overall similarity of *N. begaa* to other basal snakes
291 suggests that it occupies a position close to *Coniophis* and *Najash,* either outside of or at the
292 base of crown Serpentes. Parazygantral foramina are present in the stem snake *Najash*,
293 *Seismophis*, and Madtsoiidae, but not in the stem snake *Coniophis* and *Dinilysia* (Hsiou et al.
294 2014; Longrich et al. 2012a; Rage 1996; Rage 1975; Zaher et al. 2009), suggesting that they
295 evolved multiple times (homoplasy), or are a plesiomorphic character lost on more than one
296 occasion. Paracotylar foramina are sometimes present in *Norisophis.* They are also present in
297 *Dinilysia*, Madtsoiidae, and Simoliophiidae, all three of which may be part of the Serpentes
298 crown group (Longrich et al. 2012a). Conversely, incipient prezygapophyseal processes are
299 present in both *Norisophis* and *Dinilysia*. The weathering of the paradiapophyses on FSAC-KK
300 7001 makes it impossible to tell how well developed they are; with the exception of
301 *Tetrapodophis*, *Coniophis*, and Scolecophidia, ophidian paradiapophyses can be divided into a
302 convex diapophysis and a flat parapophysis. The small protuberances on the posterior edge of
303 the neural arch may be analogous to the low mounds described in *"Coniophis" carinatus*
304 (Hecht 1959), underscoring the need for the genus *Coniophis* be re-evaluated (Gardner &
305 Cifelli 1999). This also adds to the mounting evidence that most basal snakes are Gondwanan;
306 even though the snake total-group is potentially Laurasian in origin (Hsiang et al. 2015),
307 *Najash* and *Tetrapodophis* are Gondwanan, whilst *Coniophis* is both Gondwanan and
308 Laurasian.
309
310 5.2 Ecology of *Norisophis*.

The highly reduced neural spine is a classic feature of burrowing snakes such as *Anilius* (Hecht 1959; Apesteguía & Zaher 2006), and fossorial lepidosaurs such as amphisbaenians (Wu et al. 1996). The lateral projection of the paradiapophyses in *N. begaa* also suggests a terrestrial lifestyle, as it implies no lateral restriction of the ribs (and thus also the body) as seen in likely aquatic taxa such as *Simoliophis* and *Lunaophis aquaticus* (Rage & Escuillié 2003; Albino et al. 2016). The vertebrae also lack pachyostosis, a diving adaptation that is typical of aquatic tetrapods, including the simoliophiids (Rage et al. 2016) and *Lunaophis* (Albino et al. 2016). The scarcity of specimens is also noteworthy; the Kem-Kem is dominated by aquatic (and semiaquatic) taxa such as Simoliophiidae (Rage & Dutheil 2008), *Spinosaurus* (Ibrahim, Sereno, et al. 2014), and a large number of fish, turtle, pipid frog, and crocodyliform taxa. The rarity of *Norisophis* fossils may suggest that it was probably not aquatic, and was instead washed in from the surrounding terrestrial environment.

6. Conclusions.

As more material is discovered in the Kem Kem beds, the diversity of the snake assemblage continues to rise. With Simoliophiidae, Madtsoiidae, ?Nigerophiidae, and numerous other morphotypes (Rage & Dutheil 2008), even taking into account that different localities within the Kem Kem beds may not have been contemporaneous, niche partitioning within the localities appears to have occurred (evidence for niche partitioning in other groups has been reported; Ibrahim et al., 2016). Snake diversity appears to have been higher during the Cenomanian in Africa than in later, Maastrichtian, faunas in North America (Longrich et al. 2012b; Longrich et al. 2012a) and Europe (Rage 1996; Vasile et al. 2013). This is consistent with the idea that Gondwana played a central role in early snake evolution.

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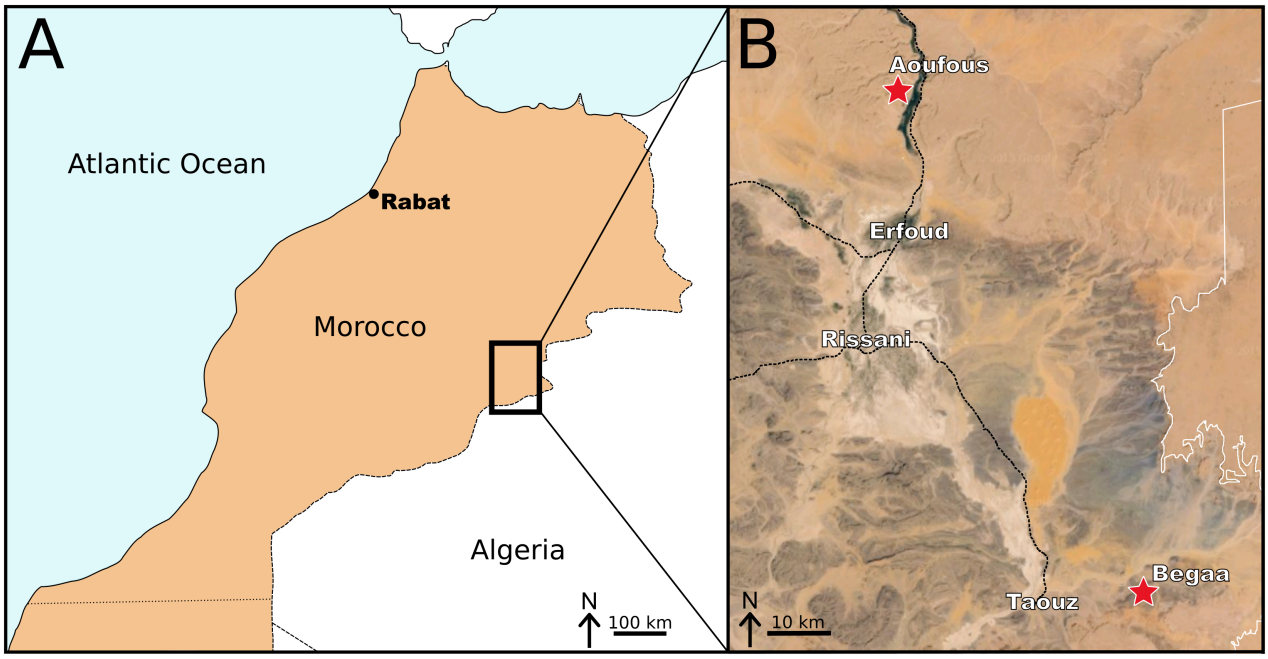


Figure 1. Map of the localities in Begaa and Aoufous, Morocco. (A) Overview of Morocco, highlighting the geographic position of the localities, and (B) satellite image of the area, with localities marked as red stars. Image from Google Maps.

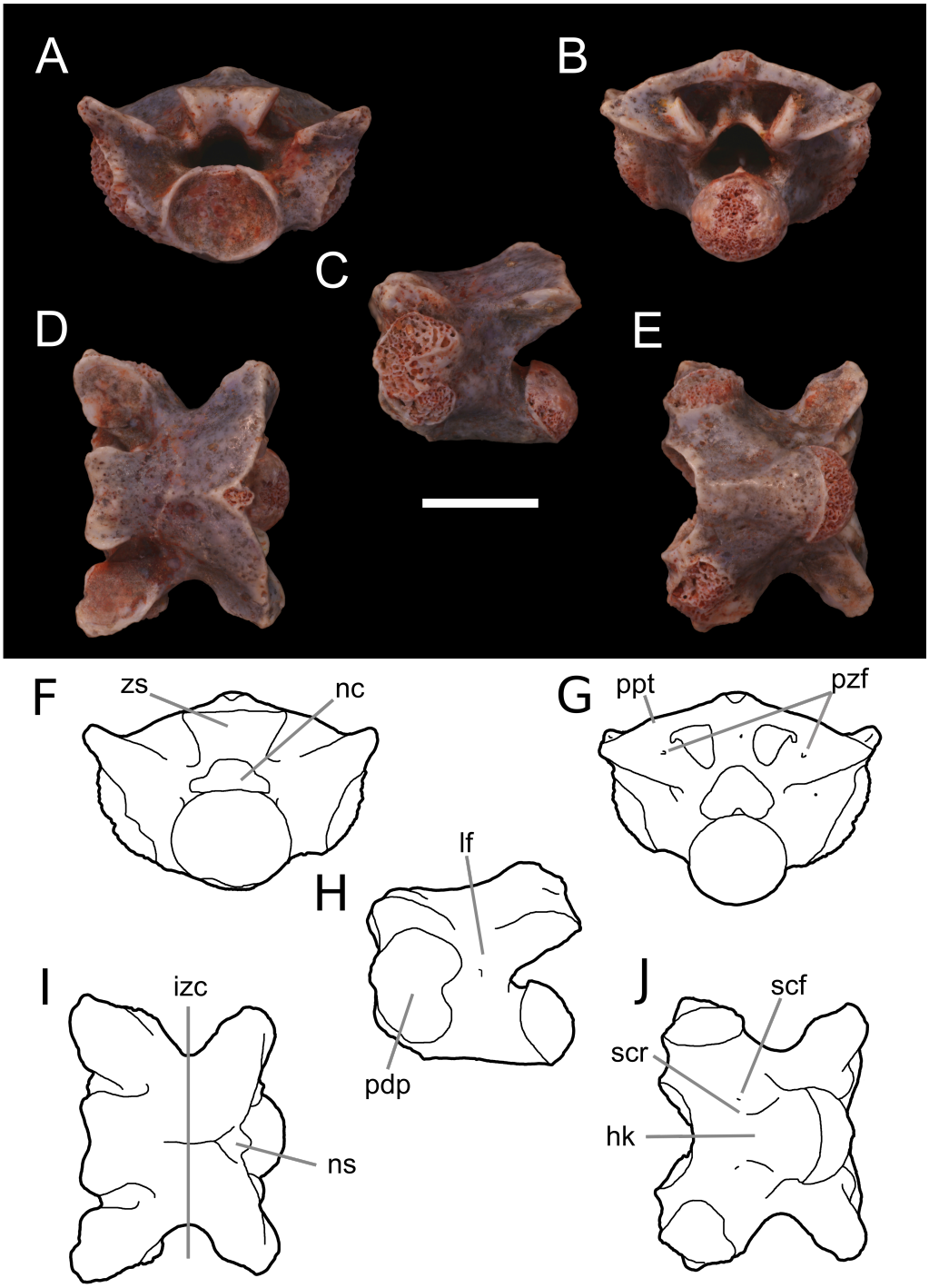


Figure 2. *Norisophis begaa* holotype, FSAC-KK 7001 in: (A,F) anterior, (B,G) posterior, (C,H) lateral (right lateral side pictured with mirror image, as it is more complete), (D,I) dorsal, and (E,J) ventral views; izc, interzygapophyseal constriction; lf, lateral foramen; nc, neural canal; ns, neural spine; pdp, paradiapophyses; ppt, pryezygapophyseal roof protuberance; pzf, parazygantral foramina; scf, subcentral foramen; scr, subcentral ridge; zs, sygosphene. Scale bar equals 5 mm.

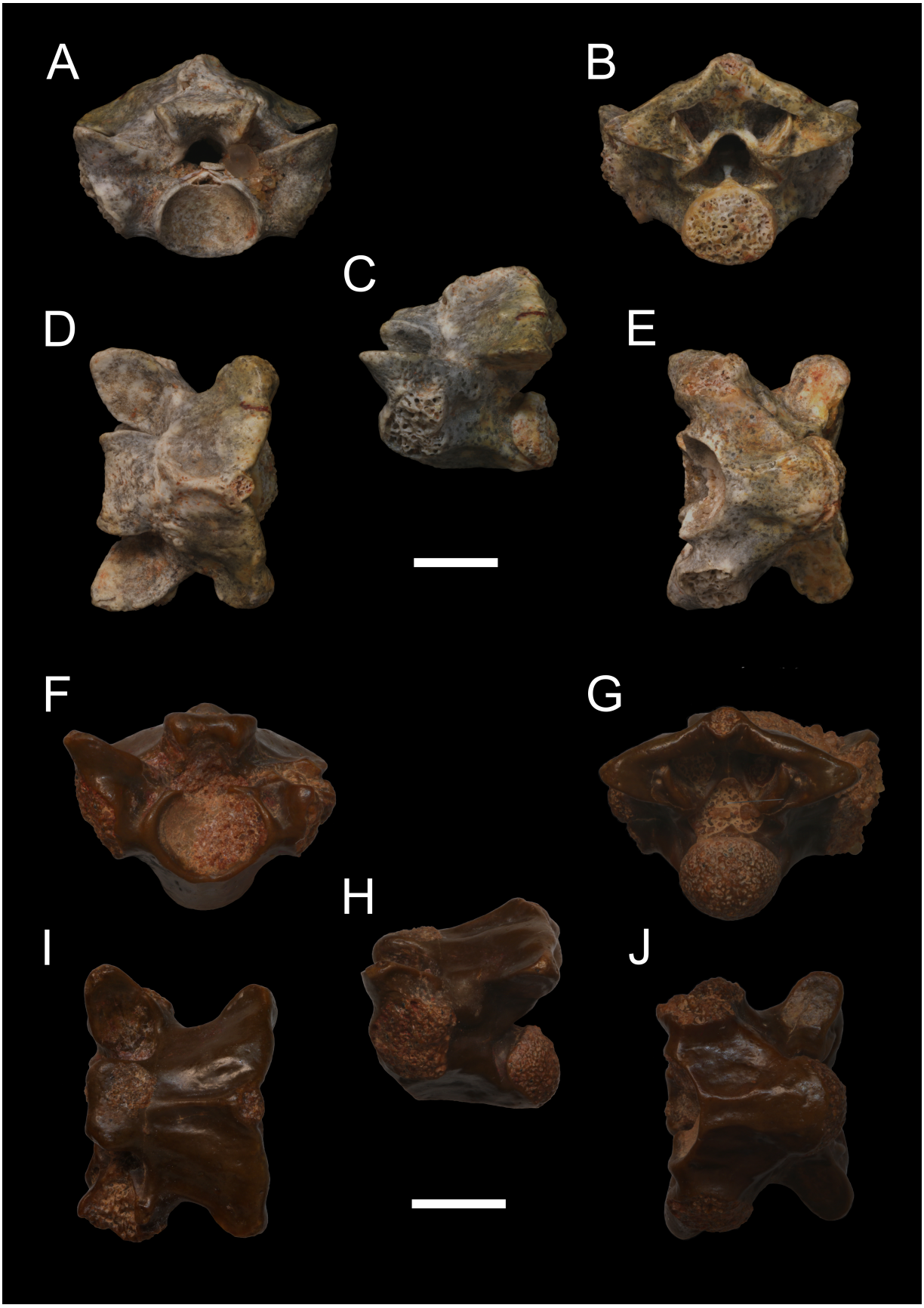
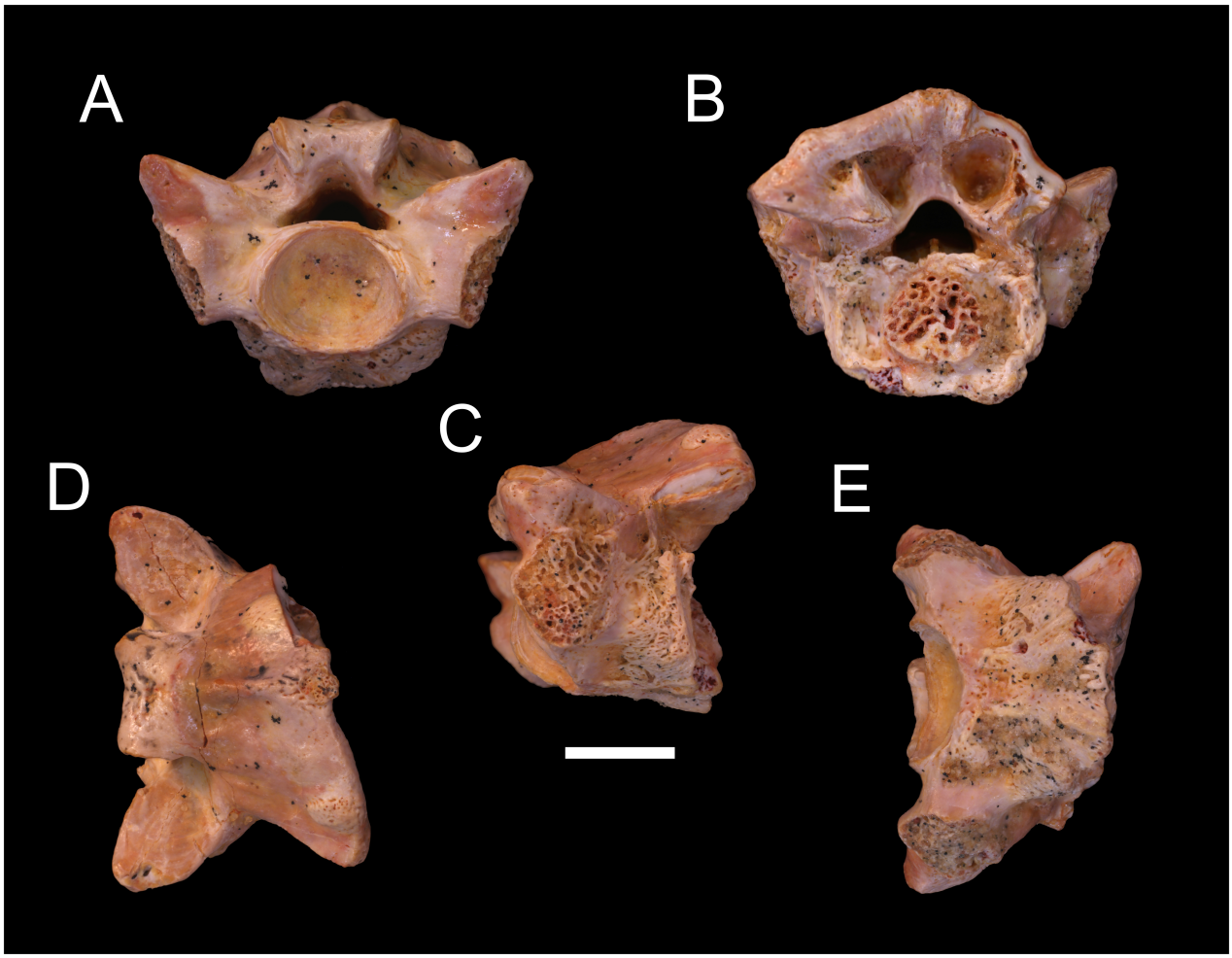


Figure 3. ***Norisophis begaa*** **paratypes,** FSAC-KK 7004 and FSAC-KK 7005 in: (A,F) anterior, (B,G) posterior, (C,H) lateral (mirror images), (D,I) dorsal, and (E,J) ventral views. Scale bar equals 5 mm.



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543 **Figure 4. Other Kem Kem snake vertebra.** (A-E) FSAC-KK 7002 a precloacal (mid-trunk)

544 *Norisophis* sp. vertebra, in (A) anterior, (B) posterior, (C) lateral, (D) dorsal, and (E) ventral

545 views. Scale bar equals 5 mm.